

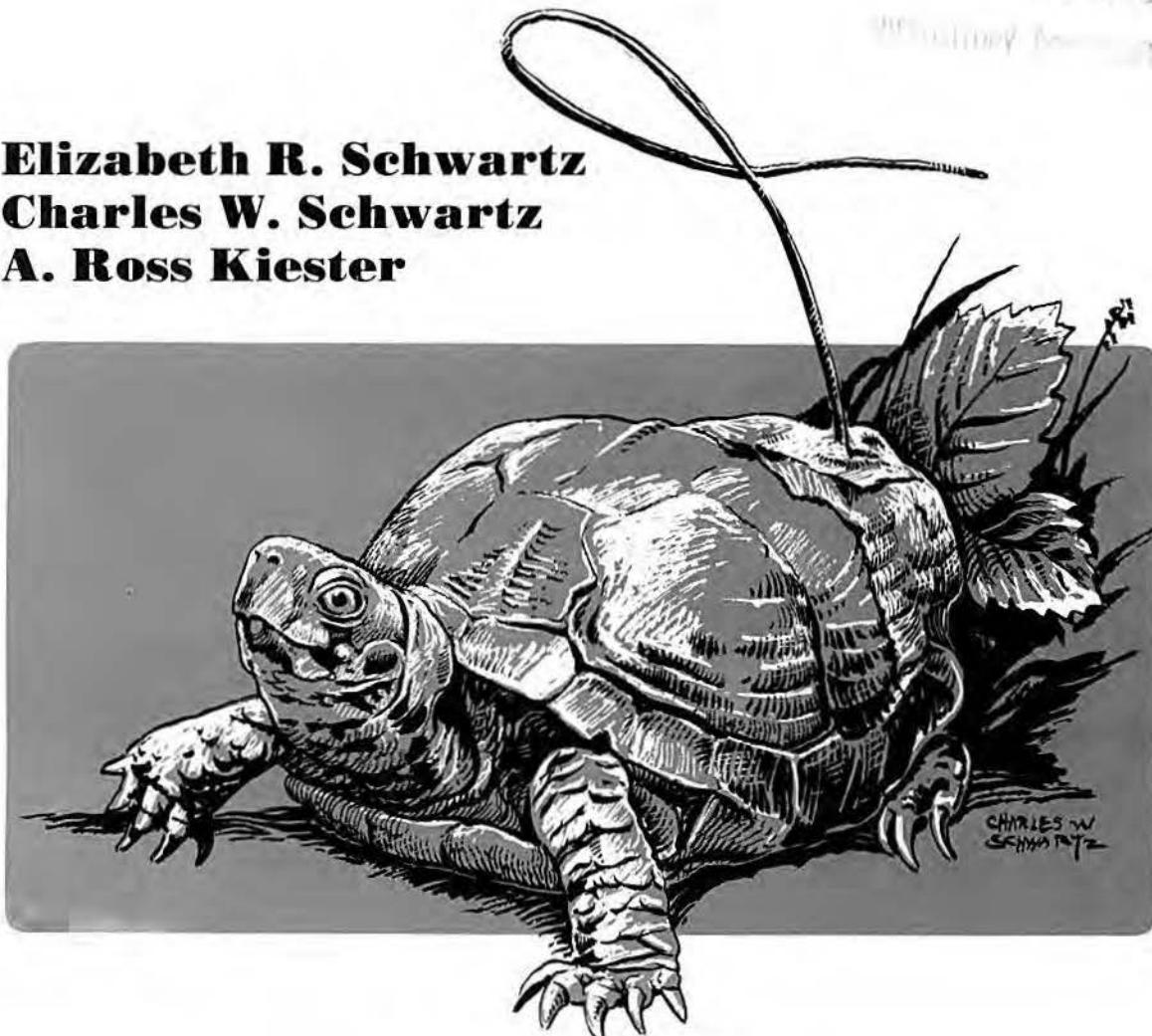
MO CON 19:12  
c. 1



# The Three-Toed Box Turtle in Central Missouri, Part II: a nineteen-year study of home range, movements and population

MISSOURI STATE LIBRARY  
APR 29 1986 283  
Jefferson City, Missouri

by **Elizabeth R. Schwartz**  
**Charles W. Schwartz**  
**A. Ross Kiester**



Terrestrial Series #12  
Missouri Department of Conservation  
Jefferson City, Missouri  
1984



## ABSTRACT

During our 19-year study from 1965 through 1983, a total of 1,568 three-toed box turtles were captured and marked on a 55-acre (22.2 ha) study area in central Missouri. Some of these were captured as many as 45 times, making a total of 5,221 recaptures and 6,789 records of individual captures.

**Age identification:** A combination of characters is presented to indicate the approximate age, or age class, of an individual. Age Class 1 comprises actively growing juveniles, usually up to 115mm in total carapace length, with obvious new growth rings on both carapace and plastron, and with increasing coloration of the carapace. Age: from hatching up through nine years. Class 2 comprises young adults, usually 115mm or more in total length, without obvious new growth rings, with wear showing on the old growth rings, particularly on the plastron, and with generally fading color of the carapace. Age: from ten through probably 32 years. Class 3 comprises old adults, usually 115mm or more in total length, with very worn to smooth carapace, smooth plastron and uniform coloration of the carapace. Age: probably 33 through at least 51 years and even more.

**Sex identification:** Because of exceptions and variations, we used a combination of several characters to identify sex externally. The presence of a depression in the plastron usually indicates an adult male and its absence, an adult female; the hind claws of adult males are usually shorter, thicker and more recurved, while those of adult females generally are longer, thinner, and not strongly recurved. Coloration of head and eyes usually indicates sex; adult males show some shade of red, while adult females show some shade of brown.

**Home range:** The average size of the home ranges of 37 long-term, permanent residents taken throughout the entire study period is 12.8 acres (5.1 ha). The average home-range size of these same turtles during their first six years was 5.3 acres (2.1 ha), showing that the average

home-range size increased during the length of the study. All occupied the same general area throughout the entire period. The average size of home range by sex was 12.9 acres (5.2 ha) for males and 12.7 acres (5.1 ha) for females. The average size of home range for Class 1 was 4.2 acres (1.7 ha); for Class 2, 9.2 acres (3.7 ha); and for Class 3, 8.9 acres (3.6 ha). Thus, juvenile turtles expand their home ranges as they grow older. Once a turtle establishes a home range, it becomes so well acquainted with the features of it that gradual successional changes in the vegetation are tolerated and have little influence on home-range size. However, when arboreal vegetation increases in open fields, turtles living in adjacent habitat may extend their home ranges into these areas.

**Movements:** Certain turtles are permanent residents in our population, while others leave. Both young and adults die, some young turtles (juvenile transients) shift their residence before establishing a permanent home range, and yet others are boundary residents or adult transients. Adult male transients are extremely important because they are the mechanism by which genes are transferred from one sedentary population to another and are thus influential in the evolution of the species.

**Population:** The population was estimated to fluctuate between 400 and 600 turtles for the first 16 years of the study. This indicates that the population remained fairly stable. Each year's population contains some turtles marked in all of the preceding years, showing that some of the turtles entering a population stay and become permanent residents.

The estimated number of the two sexes by year is approximately equal. The estimated number of the three age classes by year is: Class 1, 46 percent; Class 2, 37 percent; and Class 3, 17 percent. The probability of survival by age class is: Class 1, 66.3 percent; Class 2, 83.4 percent; and Class 3, 85.6 percent.

# **The Three-Toed Box Turtle in Central Missouri, Part II: a nineteen-year study of home range, movements and population**

**by**  
**Elizabeth R. Schwartz**  
**Charles W. Schwartz**  
**A. Ross Kiester**

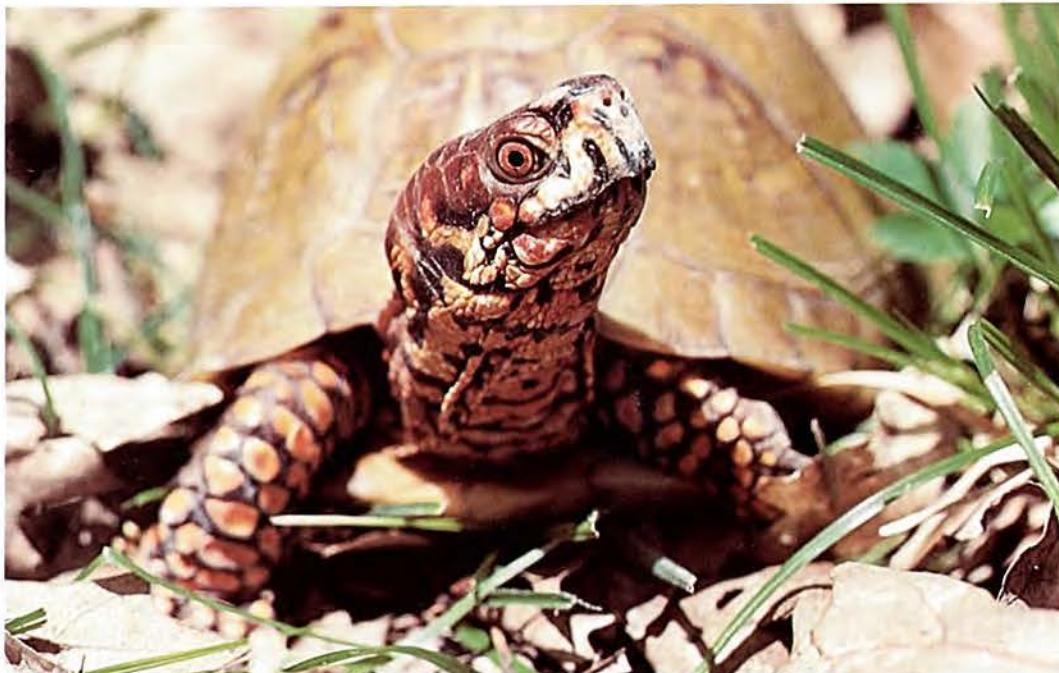
**Photographs by Charles and Elizabeth Schwartz**

**Edited & Designed by Michael McIntosh**

**Terrestrial Series #12**  
**Missouri Department of Conservation**



Copyright © 1984 by the Conservation Commission of the State of Missouri



## **CONTENTS**

- 3 Introduction**
- 5 Age Identification**
- 12 Sex Identification**
- 17 Home Range**
- 24 Movements**
- 26 Population**
- 29 Literature Cited**
- 29 Acknowledgements**



## INTRODUCTION

In 1965, when we first captured and marked turtle No. 2, he was at least 33 years old and measured 136mm in total length. His carapace was uniform olive green with wear showing on the growth rings. His plastron was yellow-green and smooth and had a slight depression. He had four legs, two front ones with five toes each, and two hind ones with three toes each—which is the basis for the common name, three-toed box turtle, and the last part of the scientific name, *Terrapene carolina triunguis*. His head was dark reddish-brown on top, but his beak, the sides of the head and his throat were marked with a distinctive pattern of orange-red, black and white. The irises of his eyes were brilliant red, one indication of his sex. Two readily discernible marks distinguish him from all other similar turtles—an unusual, naturally occurring black spot in the center of his carapace and a notch we filed in a particular marginal lamina to designate his code number.

Number Two lived in a patch of oak-hickory woods, mostly second-growth with an understory of buckbrush, catbrier, elm and redbud. Openings in the timber contained such herbaceous plants as lanceleaf ragweed and broom sedge and sprouts of elm, sassafras and persimmon. There was an intermittent drainage nearby, leading to a marshy pond.

Over the entire 19 years, our Labrador retrievers captured No. 2 a total of 44 times (Figure 1). For an entire year, from May 1970 through April 1971, we monitored his travels by means of a radio-equipped transmitter and periodically studied his daily movements by using a trailing device. His entire life during this 19-year period was spent within only 5.6 acres (2.2 ha) although he had virtually unlimited opportunity to range farther.

Now at the minimum age of 51, he is the same size, and his general appearance is similar to what it was at age 33. The black spot on his carapace has faded slightly, additional wear is obvious on the growth rings of his carapace,



Turtle No. 2

and a few blemishes have been added to his carapace. His eyes and facial markings are as brilliantly colored as ever. In 1978 his right hind leg was amputated, due to some unknown cause, but he manages to travel well on the remaining stump.

How old he really is and how old he may get to be, we can only conjecture. He may possibly reach at least 70 and even 80 years of age. This longevity ranks turtles next to man as the longest-lived, living vertebrate in Missouri.

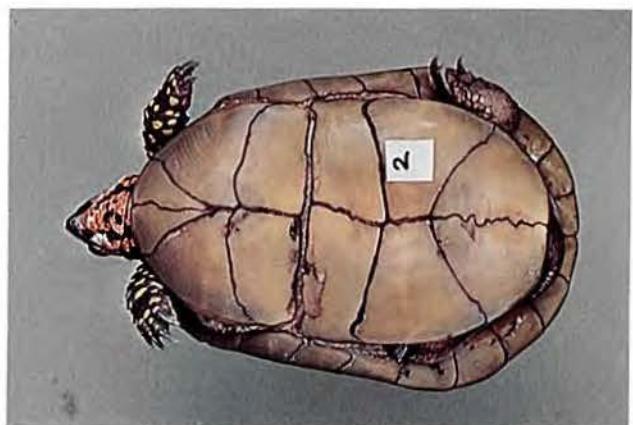
From 1965 through 1983, using our dogs, we collected and marked 1,568 different box turtles on our study area of 55 acres (22.2 ha) in central Missouri.<sup>1</sup> Some of these were recaptured a varying number of times (up to 45), making a total of 5,221 recaptures and 6,789 records of individual captures. The account of our findings from 1965 through 1973 (Schwartz and Schwartz, 1974) describes the study area and our materials and methods, including the use of our well-trained Labrador retrievers in collecting turtles. This paper discusses our techniques of aging and sexing in more detail.

This study is unique because it covers 19 continuous years of one particular wild vertebrate population and the marked individuals of this population. The propensity for some of these individuals to live in the same area for many years is noteworthy. And of evolutionary significance is the existence of transients which by their mating transfer genes from one sedentary population to another.

<sup>1</sup> Some aspects of the study were extended to 80 acres (32.4 ha).

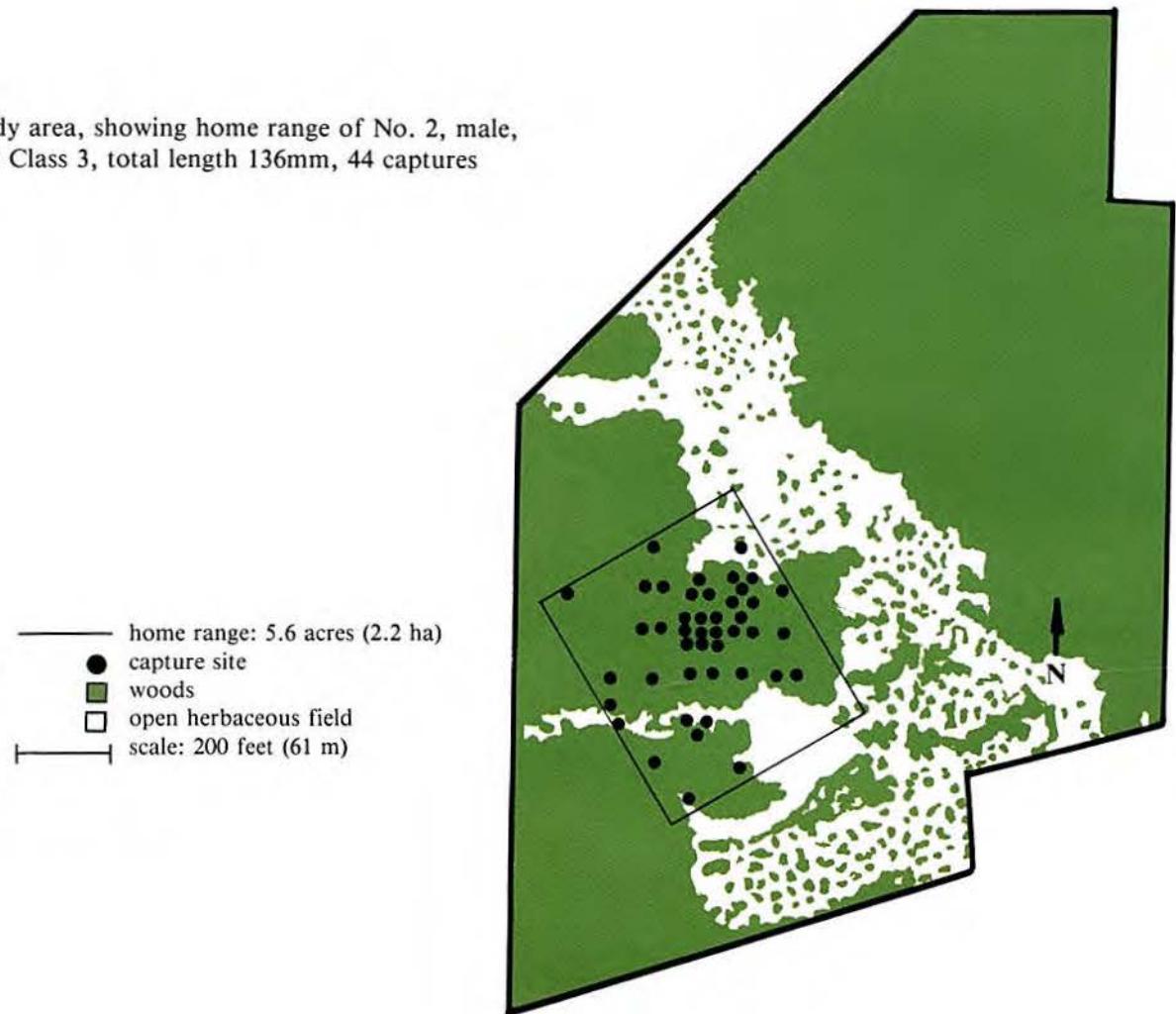


Carapace, No. 2, 1983



Plastron, No. 2, 1983

**Figure 1:** Study area, showing home range of No. 2, male,  
Age Class 3, total length 136mm, 44 captures



Year:	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
Captures:	7	3	6	3	3	1	1	1	3	1	1	1	2	2	4	1	1	0	3

## AGE IDENTIFICATION

Age identification is important in any demographic study, but in the three-toed box turtle, precise aging of randomly selected individuals in the wild is difficult. Owing to the longevity of this species, it is impractical to follow known individuals throughout their life span; therefore, we must rely upon indirect methods of aging.

Previously, the best means of aging has been a count of the annual growth rings. Nichols (1939) believes that growth rings in the Eastern box turtle (*T. c. carolina*) give a reliable accounting of age through the first five years of life, a fair degree of accuracy from ages six to nine and somewhat less up to age 15. Legler (1960) reports that growth rings in the ornate box turtle (*T. ornata*) constitute an accurate record of growth that can be studied at any time in the life of the turtle but are an accurate indicator of age only as long as regular annual growth persists. He states that growth almost stops after the thirteenth year in females and after the eleventh or twelfth years in males. By counting growth rings, Stickel (1978) establishes two major age classes in the Eastern box turtle— younger individuals (up to 20 years of age) and older individuals (21 or more years of age). She subdivides the older age class into individuals between 21 and 41 to 51 years of age (which usually have 18 to 21 growth lines that are followed by a small, tight group of at least four additional lines) and those over 41 to 51 years of age (when growth lines are no longer visible and the carapace is smooth).

Coloration of the box turtle has been described as extremely variable (Carr, 1952; Ernst and Barbour, 1972; and Conant, 1975). According to them, the carapace is brownish or greenish, usually with an irregular pattern of yellowish or orangish radiating lines, spots or splotches, and the plastron is yellow to dark brown, patternless or with dark splotches or a dark central area with branches along the seams. A correlation between color and age was



Box turtle nest and hatchlings

made by Leuck and Carpenter (1981) who report that as three-toed box turtles grow larger and older, carapace patterning fades, carapace color and margins of the plastron scutes become lighter and growth rings of the carapace scutes become less pronounced. Milstead (1969) believes that the color pattern of three-toed box turtles is genetically based.

This section of age identification deals primarily with 303 turtles from our total population which we photographed in color in addition to recording them in the usual way (measurement of total length, count of growth rings by use of a hand lens and description of coloration). The photographs were both projected and printed to help verify the count of growth rings and to serve as a visual record of the coloration, especially from year to year.

Recognizing that changes in color, wear and size are gradual and that variations occur among individuals, we believe that a combination of certain characters indicates the approximate age, or age class, of an individual. These criteria apply to turtles on our study area but may vary with other habitats of the subspecies' range due to abrasiveness of the soil over which these animals travel or to other unrecognized differences.

### By Growth Rings

#### Plates 1 and 2

In the process of growth, the germinal epithelium underneath the horny laminae of the carapace and plastron forms a new layer each year (Ewing, 1939; Nichols, 1939; Carr, 1952; Legler, 1960; and Ernst and Barbour, 1972). This is temporarily terminated when the turtle goes into hibernation, and these periods are marked by deep grooves. Growth resumes when the turtle emerges from hibernation. In spring and early summer, the new growth is only a narrow ring, but this gradually enlarges to a wider ring by fall.

Our observations indicate that a visible new growth ring is added each year until the turtle is at least nine years of age and often for a few succeeding years. In most turtles, it is difficult to be certain of more than nine annual rings, although as many as 12 or a few more can be

counted in some individuals. False growth rings, marked by shallow grooves that result from a temporary cessation of growth during the active season, sometimes make it difficult to count the true growth rings accurately.

In turtles with one to nine growth rings, the rings on both carapace and plastron are easily discernible since they show little or no wear. But as turtles acquire ten or more rings, wear (smoothness) becomes evident. This wear increases with age; it is conspicuous first on the plastron, which becomes smooth before the carapace does. In old individuals, growth rings have entirely disappeared from both carapace and plastron. Often, the outer layer of the carapace defoliates, exposing a smooth layer next to the bone or the bone itself.

## **Plate 1**

**Plates 1 and 2:** Age identification by growth rings and by the color of carapace and plastron



**Age Class 1, hatchling**



**Age Class 1, two rings  
typical color phase**



**Age Class 1, three rings  
darker color phase**



**Age Class 1, four rings  
lighter color phase**

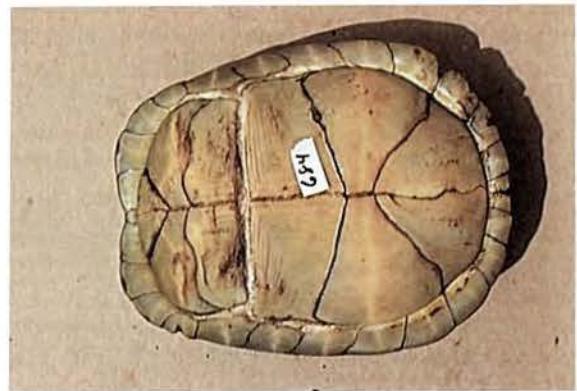


**Plate 2**

Age Class 1, nine rings



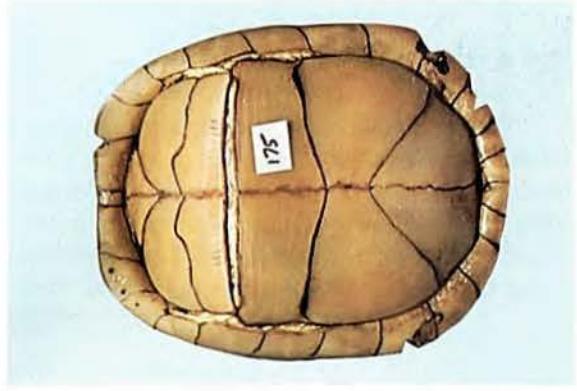
Age Class 2, early



Age Class 2, late



Age Class 3



## **By Carapace Coloration**

---

### **Plates 1 and 2**

At hatching, each lamina has a uniform dark-brown background, usually with one (or sometimes more than one) yellow or yellow-orange spot in the center. This spot is not equally prominent in all laminae.

When the turtle has acquired one growth ring (i.e., is one year of age), the background coloration of each lamina is still dark brown and the yellow spot in the center remains conspicuous, but there is a hint of other developing yellow streaks and spots.

When two rings are present, the color pattern which is typical of this subspecies appears for the first time and persists for several years. This consists of a dark-brown background, usually with a darker brown or blackish portion near the center and posterior of the lamina, and a prominent yellow spot or spots in the center of the lamina, plus additional yellow spots and streaks throughout the lamina. The streaks tend to appear as rays, since they generally extend from the center of the lamina toward the periphery. Legler (1960) suggests that this coloration somewhat matches the mottled pattern of light coming through a leafy canopy and thus provides camouflage for the turtle.

However, minor variations of lighter and darker color phases occur in this typical pattern. In some turtles, the background is a lighter brown or greenish-brown and more uniform, and the yellow spots and streaks are fewer and

fainter. These more uncolored individuals are typical of certain populations of the Eastern box turtle and occur as variations in most species of *Terrapene* (Legler, 1960).

In other individuals, the blackish background in each lamina extends farther anterior, making the general background more nearly black than dark brown. The typical coloration and its variations occur until nine or ten annual growth rings have been formed.

About the time the tenth ring is growing, the formation of additional yellow spots and streaks around the edges of the laminae slackens. The existing spots start to fade, although the yellow in the centers of the laminae remains prominent. From this stage on, these central yellow spots and streaks also fade, and the dark brown that was prominent in the posterior part of each lamina outlines the spots formerly pigmented with yellow. The general background is light brown to greenish-brown. Leuck and Carpenter (1981) suggest that this fading is caused by increased physical wear and exposure to sunlight.

The color pattern continues to fade until the carapace is uniformly colored, either brown or olive-green. Occasionally there may be faint flecks of yellow or spots of dark-brown pigment remaining in depressions, but the pattern of earlier years has vanished.

## **By Plastron Coloration**

---

### **Plates 1 and 2**

At hatching, the plastron is generally yellow with a variable smudge of brown toward the midline.

From one to nine years of age, the plastron is usually greenish to yellowish. The newest growth ring is conspicuous on the growing margins of each lamina, especially on the anterior and medial margins, and varies in color from whitish to pinkish to yellowish. There is a tendency

for most turtles to have a narrow to wide, dark-brown to blackish border on the posterior portion of most laminae. In some turtles, a smudge of brown is present in various laminae.

In older individuals, when growth lines are very faint or obliterated, the plastrons are uniformly colored, yellow, yellow-green or olive-green.

## **By Carapace Length**

---

The total length of the carapace compared to the age classes (see Age Classes) is given in Figure 2. Average size tends to increase progressively until turtles have nine or more rings. At this time, growth slows down or almost ceases, although a little growth may occur in later years under favorable environmental conditions. Because all in-

dividuals do not grow at the same rate, size alone does not indicate age. Legler (1960) reports a similar condition in the ornate box turtle and believes that size is related more to the attainment of sexual maturity than to age.

Females tend to attain a larger size than males.

## Age Classes

We established three age classes on the basis of the number and condition of growth rings, coloration and total length. These are described in Table 1. The age class is easy to identify in most individuals, but occasionally, a turtle in transition may be difficult to place in the correct class.

By applying this age classification to our population of 1,568 turtles, we can estimate the time span for each age class. Forty-one individuals marked at the beginning of

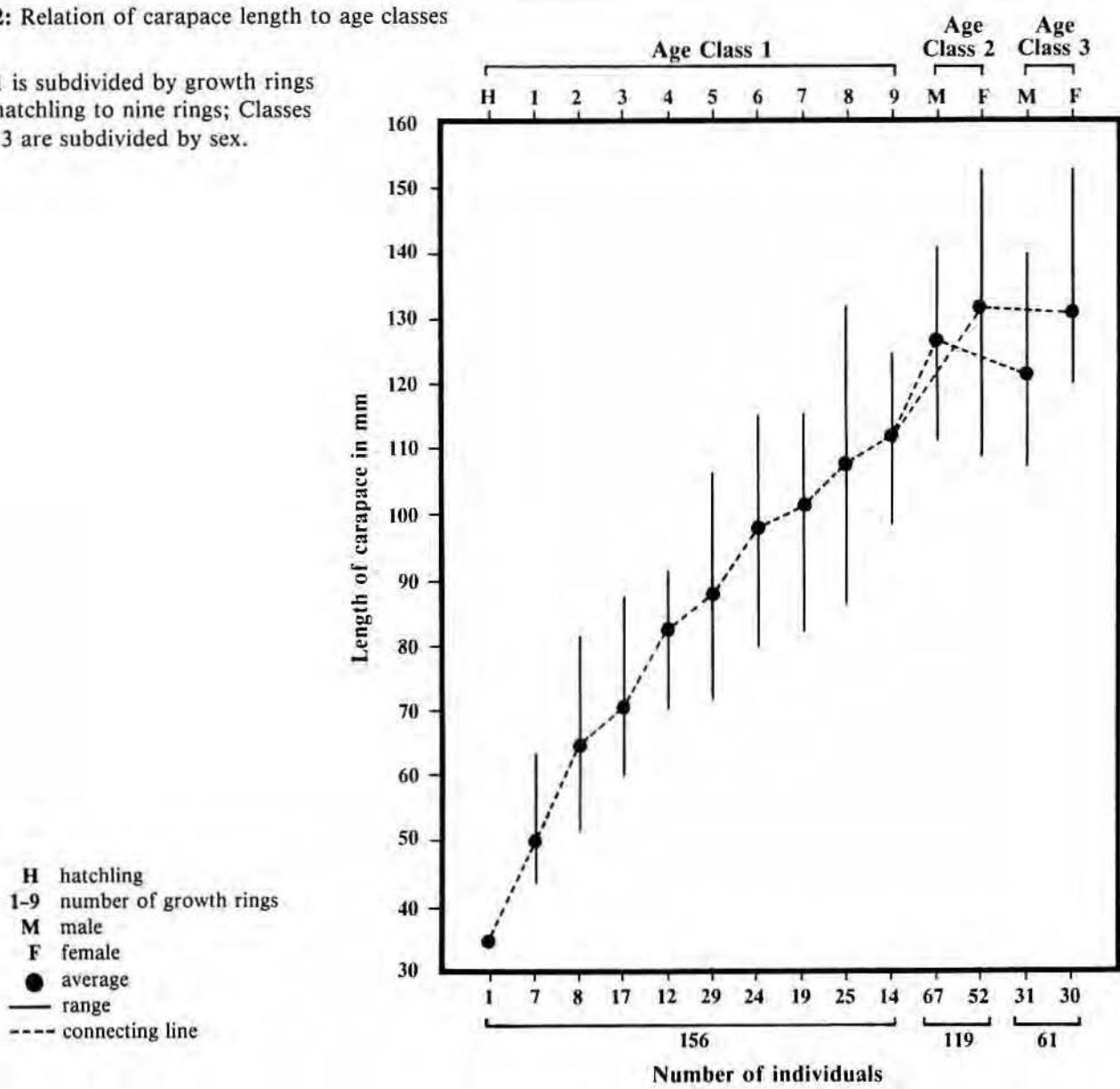
our study remained in the population until the end of the study.<sup>2</sup> We call this group "long-term, permanent residents." Of these 41 turtles, six were in Class 1 when first collected; these all changed to Class 2 and remained in Class 2. Of 23 turtles that were in Class 2 when first collected, five were still in Class 2 at the end of the study, while 18 changed to Class 3 and stayed in that class. The 12 turtles in Class 3 when first collected stayed in Class 3.

We estimate the duration of the respective age classes

<sup>2</sup> We consider that it required the first two years to mark our population, so turtles marked in 1965 and 1966 constitute the original population. Forty-one turtles marked in these years were retaken during the last two years of the study. Twenty-two were collected over 19 years, and all of these were marked in 1965 and last taken in 1983. Nineteen were collected over 18 years, but of these, 11 were marked in 1965 and last taken in 1982, and eight were marked in 1966 and last taken in 1983.

Figure 2: Relation of carapace length to age classes

Class 1 is subdivided by growth rings from hatching to nine rings; Classes 2 and 3 are subdivided by sex.



**Table 1:**  
Age classes  
of the  
three-toed  
box turtle

Age Class	Growth Rings			Color		Total length of carapace
	Number	New Growth	Wear	Carapace	Plastron	
<b>1. Juveniles</b> (actively growing); duration, 9 years; from hatching through 9 years of age	up through 9	always present; most conspicuous in fall	little or none	each lamina with light- to dark-brown or black background, usually darker toward posterior of lamina, and variable number of yellow spots and streaks; rarely greenish-brown background with few yellow spots	yellow, yellow-green or olive-green, may be uniform or have a dark-brown or black border on posterior edge of most laminae; may have smudge of brown	usually up to 115mm (rarely larger in oldest juveniles)
<b>2. Young adults</b> (growing slowly or have recently stopped growing); duration, probably 23 years; from 10 through 32 years of age	when visible, 10 or more; usually cannot be counted because of wear	usually not present; if present, narrow and inconspicuous	varies from beginning to show wear to badly worn; some plastrons may be worn smooth	each lamina with brownish or greenish background and yellow spots and streaks which are beginning to fade and to be replaced by light brownish- or yellowish-green	yellow, yellow-green or olive-green, usually uniform but may have a dark-brown or black border on posterior edge of some laminae; may have smudge of brown	usually 115mm or more (rarely smaller)
<b>3. Old adults</b> (have not grown for some time); duration, at least 19 years but probably longer; from 33 through at least 51 years of age	cannot be counted because of wear	not present	carapace badly worn to smooth; all plastrons smooth	uniform brown or olive-green	uniform yellow, yellow-green or olive-green	usually 115mm or more (rarely smaller)

as follows. Class 1 lasts for nine years by our definition of adding one growth ring for each year of age. Class 2 encompasses at least 19 years, because five turtles in this class at the beginning of our study were still in Class 2 at the end of the study. If we assume that the age distribution of the turtles in Class 2 at the beginning of the study was random and since 18 of the 23 turtles passed on to Class 3 during the study, then the remaining five turtles (22 percent of 23 turtles) will require four more years (22 percent of 19 years) to pass into Class 3, making a likely duration of 23 years for Class 2. Class 3 lasts for a known 19 years and probably more. Thus, our oldest turtles are at least 51 years old—nine years in Class 1, 23 years in Class 2 and 19 years in Class 3. However, if the oldest turtle we marked in 1965 was at least 51 years old and was still alive in 1983, this turtle could possibly be 70 years of age. But it seems

unlikely that many turtles reach this age. This longevity is comparable to estimates made by others which vary from 50 to more than 80 years (Nichols, 1939; Legler, 1960; and Stickel, 1978).

Our three age classes in the three-toed box turtle are roughly comparable to Stickel's three age distinctions in the Eastern box turtle; differences lie in the span of the respective ages. Because growth rings in the Eastern box turtle are formed over a longer period (up to six to eight years after puberty, according to Nichols, 1939) and are visible longer, Stickel can identify growing individuals until at least 20 years of age, which we cannot do. Also, her study covered 30 years, which enabled her to establish with certainty a greater maximum age for this subspecies' life span.



This turtle, inscribed by Robert Bassman on April 30, 1937, was found on July 10, 1967, approximately  $1\frac{1}{2}$  miles (2.4 km) from its initial capture and release site in a suburban area of Jefferson City, Cole County, Missouri. The original incising was deep, but over the years the edges became worn and, in some places, were barely visible. The turtle must have been fully grown at the time of marking, because the letters filled most of the laminae. A minimum estimate of its age in 1967 was 40 years (at least 10 years are required to reach adult size, plus a 30-year interval between marking and recapture), but the turtle probably was considerably older.

The age of this turtle agrees with other reports we have received of similarly marked turtles being recovered between 32 and 51 years later. Although these popular reports could lack some credibility, they seem reasonable nevertheless in light of technical data.

## SEX IDENTIFICATION

The absolute way to sex a three-toed box turtle is by the presence of testes, penis or ovaries. Testes and ovaries can be identified only upon dissection. The penis can be seen upon dissection, but in some live turtles it is extruded when handled. Also, its position may be observable as a bulge at the base of the tail. However, failure to observe these external sex indicators does not mean that the turtle is a female.

In males, the vent opens slightly nearer the tip of the tail than it does in females, but because the tails are usually

contracted, this opening is hard to identify.

We used highway-killed specimens to compare the sex organs with certain external sexual characteristics. Although we found no reliable way to identify the sexes externally, by using a combination of several external characters we feel that our identification is as accurate as possible. Other workers, likewise, have used various secondary sexual characteristics with varying degrees of success (Nichols, 1940; Dolbeer, 1969; Reagan, 1974; and Leuck and Carpenter, 1981).

### By A Depression in the Plastron

When a turtle is withdrawn into its shell, the only way to identify the sex is by the presence (male) or absence (female) of a depression in the posterior lobe of the plastron. This is more reliable in older turtles (those without new growth rings on the plastron, i.e., older members of Class 2 and all of Class 3) but is not reliable in turtles with new growth on the plastron (Class 1 and the younger members of Class 2). Some males' plastra may

have no depression (verified by highway-killed males) and some turtles have "questionable" depressions; these latter may be either males or females. When the depression is questionable, a female tends to have a wider plastron which is convex at the extreme edges, while a male has a narrower plastron which is flatter at the edges. But in most adults, the presence of a depression indicates a male and its absence a female.



Plastron  
with depression,  
male



Plastron  
without  
depression,  
female

### By Hind Claws

When the turtle emerges from its shell, the hind claws can be observed, and in larger, older turtles these often, but not always, show a difference according to sex. In older turtles, females have longer, thinner claws that are not strongly recurved, while males have shorter, thicker

claws that are strongly recurved. In younger turtles, the heavy claws do not develop in males until other secondary sexual characters are fairly well established. This claw development is controlled by the male sex hormone, testosterone (Evans, 1952).



Male



Female

### Plate 3

Sex identification by color of the head and iris of the eye:  
Age Class 1

The heads of turtles in Age Class 1 with one through five growth rings are predominantly brownish with light yellow, primarily on beak and throat. Some turtles (presumably females) with six through nine rings show this color while others (presumably males) show an increase in red, black and more brilliant yellow and orange.

Predominant eye color is yellowish- or blackish-brown, but dark red appears in the older turtles that presumably are males.



Age Class 1, one ring



Age Class 1

two rings



three rings



Age Class 1, six rings

presumably female



presumably male



Age Class 1, eight rings

presumably female



presumably male



Age Class 2

#### Plate 4

Sex identification by color of the head and iris of the eye:  
Age Classes 2 and 3, females

The heads of females in Age Classes 2 and 3 are variable but tend to be yellowish-brown to blackish-brown, sometimes marked with black, white, yellow or yellow-orange. The eyes are some shade of brown, rarely dark reddish-brown. They may be uniform, mottled or show rings of yellow, gold, orange, blue, pale red or purple.



Age Class 2



Age Class 2



Age Class 2



Age Class 2



Age Class 2



Age Class 3

## Plate 5

Sex identification by color of the head and iris of the eye:  
Age Classes 2 and 3, males

The heads of males in Age Classes 2 and 3 are variable but usually are reddish-brown with markings of orange-red, white and yellow. The eyes usually are bright red to light red; they may be uniform, mottled or show rings of yellow, white, purple or purple-brown.



Age Class 2



Age Class 2



Age Class 2



Age Class 2



Age Class 3



Age Class 3



Age Class 3

## **By Head Coloration**

---

### **Plates 3, 4 and 5**

When the head protrudes out of the shell, it is possible to see the color of the head and eyes. Color generally indicates sex, particularly in older turtles, and shows differences with age.

With an occasional exception, the heads of all turtles in Class 1 having one through five growth rings are similarly colored. They are predominantly yellowish-brown to blackish-brown with some very light yellow, primarily on the beak and throat. Turtles in Class 1 from about six through nine growth rings are of two general types: (1) those (presumably males) that show an increase in reddish coloration, stronger black and more brilliant yellow and orange; and (2) those (presumably females) that are either still colored like the younger stages or, if more strongly colored with black, white or yellow, lack a reddish cast. In ornate box turtles, sexual maturity of most males occurs in the eighth and ninth years and of most females in the tenth and eleventh years, although in some individuals it begins three to four years sooner than the average (Legler, 1960). In three-toed box turtles, it may be assumed that with the approach of sexual maturity males begin to develop more coloration, primarily reddish, in response to increasing levels of testosterone. The amount of coloration is variable, but during these ages the sex probably can be determined fairly accurately by coloration.

Classes 2 and 3 are considered together because once a turtle reaches the size of these classes, sexual maturity

presumably has been reached and the coloration of males has been determined. In Classes 2 and 3, the males' heads may be blackish or brownish, but they usually are reddish-brown, and their beaks, throats and sides of the head may have considerable orange-red with black, white and yellow markings. Rarely there are spots of yellow, orange or red on top of the head. The beaks, particularly of males but sometimes of females, are often boldly marked and have an individual pattern that remains constant for as many years as we have observed the various individuals. It is significant that the markings and coloration are distinctive in all adult males. In these classes, the females' heads generally are colored like the young turtles in Class 1 that presumably were females; their overall color is a yellow-brown to black-brown, although some may have black, white, yellow or yellow-orange on their beaks, throats or sides of the head. Rarely there are spots of yellow-orange on top of the head. In boldly marked adult females, too, the individuals are distinctive.

We find only minor differences in the coloration of individuals in these classes when photographed over a period of years. (Intensive photographic records have been made for the past seven years, but we have photographic records for some individuals up to 19 years.) Coloration does not fade with increasing age and is as brilliant in male turtles considered very old as in males that may be several decades younger.

## **By Eye Coloration**

---

### **Plates 3, 4 and 5**

We examined the eyes of most of our turtles in life and photographed the eyes of 303 individuals, representing both sexes and the three age classes. In addition, we recorded the iris color of 38 fresh, highway-killed turtles and related it to sex as determined by internal examination.

Our findings show that, in general, adult male (Classes 2 and 3) irises have some shade of red, varying from bright red to light red. Sometimes this color is uniform; sometimes the red is mottled with yellow, white or purple to purple-brown; and sometimes it is nearly uniform with a ring of one of these colors on the outside margin or around the pupil or both.

The predominant color of the irises of adult females is generally some shade of brown, varying from yellowish- to reddish-brown. This color may be nearly uniform; splotched with various shades of yellow or gold, orange, blue, pale red or purple; or nearly uniform with rings of one or more of these colors around the outside margin or the pupil. Rarely, a female's irises may be yellowish splotched with purple or they may be red, darker and browner than the males' red irises. These variations have also been reported by Nichols (1940).

The predominant iris color of young turtles (until about five annual growth rings are present) is yellowish- or

blackish-brown, but sometimes it is yellowish. In young turtles from about six through nine growth rings, these same colors occur, but reddish-brown and dark red start to appear in turtles that presumably are males. All of these irises may be uniform, splotched or nearly uniform with rings of various colors similar to those of adults.

We have combined the many variations to these generalities in order to have a workable description. There are, however, a few exceptions to this general classification. These may result from our inability to discern the correct shade of color, from incorrect sex identification in the living animal or from the variability of the male hormone which, according to Evans (1952), controls the development of red pigment in the males' irises.

Head and eye coloration is, in part, an external indication of sexual maturity and is used in courtship, when the male reportedly displays his colored throat to the female (Ernst and Barbour, 1972). But coloration may have an additional function. Turtles have excellent color perception and can learn to recognize all colors as well as black and white (Pope, 1939; Burghardt, 1977), more readily identifying colors near the red end of the spectrum (Pope, 1939). For example, Casteel (1911) trained painted turtles (*Chrysemys picta*) to distinguish between black and white

and between both horizontal and vertical lines of varying widths. This ability to learn to distinguish colors and lines of differing widths, coupled with the extraordinary variation in head color and marking, suggests that box turtles may learn to recognize individuals. Individual recognition has yet to be conclusively proven for a reptile (Kiester,

1977), but we hypothesize that turtles living together in the same general area for many years (see Home Range) are capable of recognizing each other and likewise of identifying a stranger. An experimental test of this hypothesis awaits further research.

## HOME RANGE

One phase of our research concerned the box turtle's home range—the area within which an individual lives and performs all of its activities. In our 1974 paper, we reported home-range data over the six-year period from 1965 through 1970; with the continuation of our study, we have accumulated data for a 19-year span in the life of this long-lived animal.

Our population figures show that some individuals remained in our research area during the entire study period while others disappeared. Of the 41 individuals present

from the beginning to the end of our study (see p. 9), we selected 37 that had been most often captured by our dogs (11 to 44 times<sup>1</sup>). We wanted to learn where they lived during this entire period; the size of their home ranges; if there was any relation between home-range size and the individual's sex or age; and what relation there might be between population density, home-range size and vegetation.

<sup>1</sup>This is the maximum number of times captured for the permanent resident group. Forty-five was the maximum in the population as a whole.

### Size and Location of the Home Range

The average size of the home range of these long-term, permanent residents is 12.8 acres (5.1 ha). The extremes range from 1.6 to 26.4 acres (0.6–10.6 ha).

To determine if the size of the home range varied with time, we singled out the first six-year home-range sizes of these turtles and compared them with their 18- to 19-year home-range sizes (Figure 3). The average six-year home-range size was 5.3 acres (2.1 ha), with extremes of 0.2 and 13.8 acres (0.08–5.5 ha). The size of the home range of all but one individual increased during the course of the study; that of the one exception remained the same.

In our 1974 paper, we reported the average home range of 239 adult turtles taken between four and eighteen times from 1965 through 1970 to be from 2.9 to 11.6 acres (1.1–4.6 ha).

The increase in home-range size shown in the long-term study might be related (1) to the longer period over which the turtles were captured, reflecting a more accurate picture of the range size; (2) to an increase in general activity related to a change in age or to vegetative changes in the habitat (both discussed below); or (3) to an increase in the number of times captured. While the number of times captured may influence the size of the range, turtles having the largest home ranges—more than 24 acres (9.7 ha)—were captured 13, 18, 21 and 31 times; those occupying the smallest home ranges—less than six acres (2.4 ha)—were captured 12, 16, 32, 36, 43 and 44 times.

Stickel (1978) reports that the home ranges of her marked Eastern box turtle population were essentially the same size in 1975 as in 1945.

In this group of long-term, permanent residents, we compared the location of the home ranges during the first six years with those during the following years. All of these



Turtle No. 8071, with radio transmitter

turtles continued to occupy the same general area during the entire period.

To further understand the size and location of the home range, we compared a yearly home range with the total 18- to 19-year home range. Eight turtles were studied by transmitter for periods up to one year. Turtle No. 2 (Class 3, male) lived in 4.9 acres (1.9 ha) during the year he was equipped with a transmitter, while he occupied a total of 5.6 acres (2.2 ha), computed from dog capture over 19 years. Turtle No. 91 (Class 3, female) restricted her activity to 1.8 acres (0.7 ha) while radio-tracked during three months of one year; her home range by dog capture for 18 years was 4.8 acres (1.9 ha). Turtle No. 164 (Class 3, female) was radio-tracked for 62 days in one year. Her home range during this time was 17.7 acres (7.1 ha), compared to a 19-year home range of 15.7 acres (6.3 ha), computed by dog capture. Five other turtles—No. 9, Class 3, male; No. 21, Class 2, female; No. 25, Class 3, male; No. 80, Class 2, female; and No. 151, Class 2, male—reported

below as controls for our study of transients, also had yearly home ranges smaller than their total ones computed by dog capture.

Unquestionably, these turtles are familiar with the physical aspects of their home ranges as they affect their lives; this is indicated by their return to specific resting spots from time to time and by the utilization of certain

paths around obstacles, such as down logs. Because their home ranges show considerable overlapping, each turtle probably is well acquainted with its turtle neighbors and encounters them frequently. We occasionally find two and even three radio-equipped turtles bedded side by side and have observed two turtles—bearing transmitters—hibernating next to each other.

**Figure 3:** Size of six-year home range (1965–1970) compared to nineteen-year home range (1965–1983); turtle No. 165, female, Age Class 3, total length 125mm



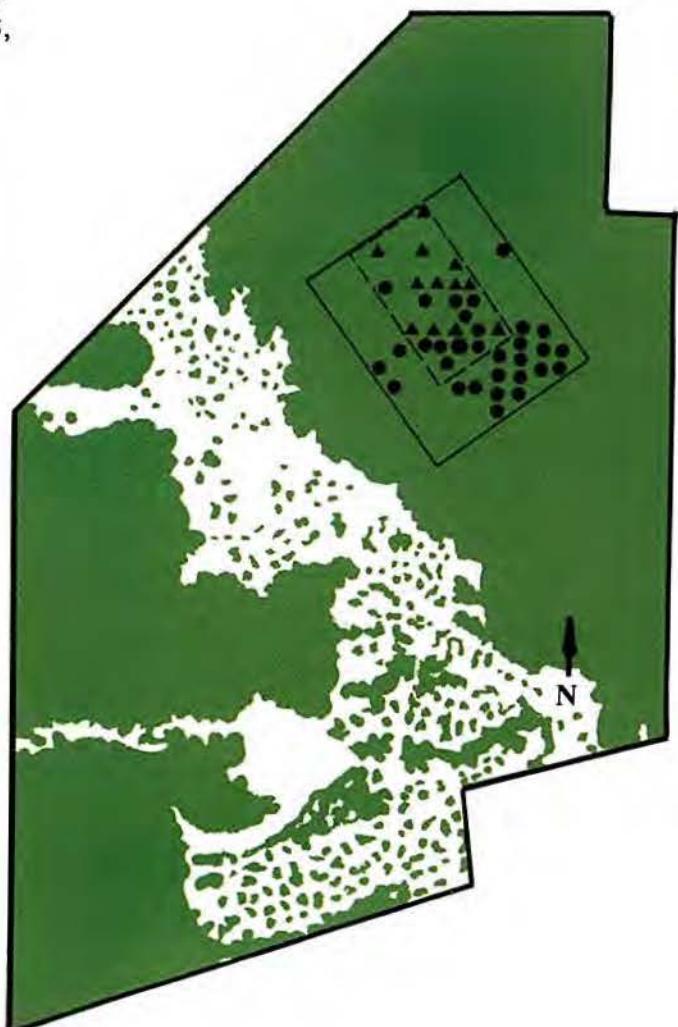
Turtle No. 165

- home range 1965–1970, 1.5 acres (0.6 ha)
- home range 1965–1983, 4.6 acres (1.8 ha)
- ▲ capture site 1965–1970
- capture site 1971–1983
- woods
- open herbaceous field
- scale: 200 feet (61 m)

43 captures: 12 in first six years; 31 in last 13 years

Year:	1965	1966	1967	1968	1969	1970
Captures:	3	4	0	4	0	1

Year:	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
Captures:	2	2	2	5	4	5	3	4	1	1	0	1	1



### Size and Location of the Home Range in Relation to Sex

The average home-range size of the permanent-resident sample was nearly the same for the two sexes—12.9 acres (5.2 ha) for 21 males and 12.7 acres (5.1 ha) for 16 females. Extremes for males were 1.6 and 25.2 acres (0.6–10.2 ha) and for females 4.6 and 26.4 acres (1.8–10.6 ha).

In our 1974 paper, we reported the average size of the

home range for the two sexes to be nearly the same (3.8 acres, 1.5 ha, for 79 males and 3.6 acres, 1.4 ha, for 64 females). We interpret the present increase in average home-range size by sex to reflect the general increase in size of the home ranges over the 19-year period.

The locations of the home ranges of the same and different sexes broadly overlap.

## Size and Location of the Home Range in Relation to Age Class

(See page 9)

**Adults:** In our long-term, resident group, five turtles stayed in Class 2 for the entire 19 years; four changed from Class 1 to Class 2 (and were taken four or more times in Class 2); and 13 changed from Class 2 to Class 3 (and were taken four or more times in Class 2). The average home-range size for these 22 turtles while they were in Class 2 was 9.2 acres (3.7 ha), with extremes of 1.6 and 24.2 acres (0.6–9.8 ha).

Ten turtles were in Class 3 for the entire 19 years, and 13 changed from Class 2 to Class 3 (and were taken four or more times in Class 3). The average home-range size for these 23 turtles while they were in Class 3 was 8.9 acres (3.6 ha), with extremes of 1.8 and 26.4 acres (0.7–10.6 ha).

The average home-range sizes for Classes 2 and 3 are nearly the same, indicating that younger and older adults have the same size home range. Both age classes occupy the same general location.

**Juveniles:** Six of the permanent-resident group chang-

ed from Class 1 to Class 2 during the 19-year period. Four of these were taken four or more times in both classes. Their Class-1 ranges averaged 1.8 acres (0.7 ha), while their Class-2 ranges averaged 10.9 acres (4.4 ha). The ranges of these individuals while in Class 2 were in the same locality as their Class-1 ranges and included from half to all of that class's range (Figure 4).

To study the size of the home range of very young turtles (with two to five rings at the time of capture), we examined 15 individuals that were taken six or more times in Class 1. Their home ranges averaged 4.2 acres (1.7 ha) and varied from 0.8 to 9.2 acres (0.3–3.7 ha). Six members of this group changed to Class 2 during our study. Their capture points in this new class were within their Class-1 range or nearby; the farthest was 300 feet (91.5 m) away.

The home range of a different group of ten juveniles reported in our 1974 paper varied from less than one acre through eight acres (0.4–3.2 ha).

**Figure 4:** Size of home range in Age Class 1 compared to that in Age Class 2 for turtle No. 514, male. Total length: first capture, 97mm; last capture, 131mm



Turtle No. 514

- home range, Age Class 1, 2.1 acres (0.8 ha)
- home range, Age Class 2, 12.6 acres (5 ha)
- ▲ capture site, Age Class 1
- capture site, Age Class 2
- woods
- open herbaceous field
- scale: 200 feet (61 m)

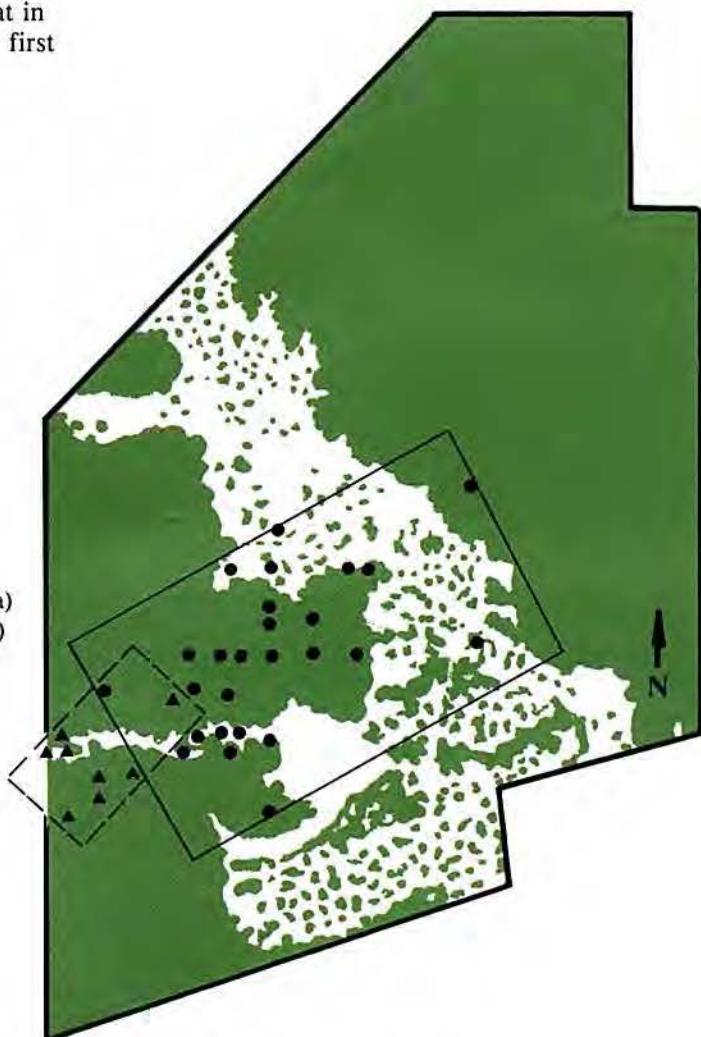
34 captures: 8 in Class 1; 26 in Class 2

### Age Class 1

Year:	1965	1966	1967
Captures:	1	1	6

### Age Class 2

Year:	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
Captures:	1	0	0	0	3	1	2	2	3	5	2	4	1	0	1	1



Thus, as juvenile turtles grow older, they expand the size of their range but continue to use the same vicinity.

We have no data on the home range of hatchling turtles, but Madden (1975) radio-tracked hatchlings and found that in their first three seasons of activity, hatchlings traveled no farther than the woods surrounding the fields containing their nesting site; he also found that though hatchlings' habitat requirements are similar to those of adults, they move less and have smaller home ranges.

One of our turtles, No. 6015, which had two rings at the time of capture and was discussed at greater length in our 1974 paper, is still in the study-area population. This individual, equipped with radio, was monitored from 23 July to 27 September 1973 (Figure 5). Its home range during this time covered 0.4 acre (0.1 ha). After 27 September,

no signal was received, and 6015's whereabouts were unknown. This turtle was captured by our dogs in October 1974 approximately 1,000 feet (305 m) from its last known location. Thereafter, it was taken each year from 1975 through 1979 and again in 1982. From 1974 through 1982, it occupied a home range of 5.0 acres (2.0 ha), showing that once this turtle selected its permanent residence, it continued to live there through the succeeding years.

From our data, we conclude that there is an increase in average home-range size from Class 1 to Class 2 but that the average home-range sizes of Classes 2 and 3 are nearly the same. Also, once an individual becomes a permanent resident, it continues to live in the same general vicinity as it grows older.

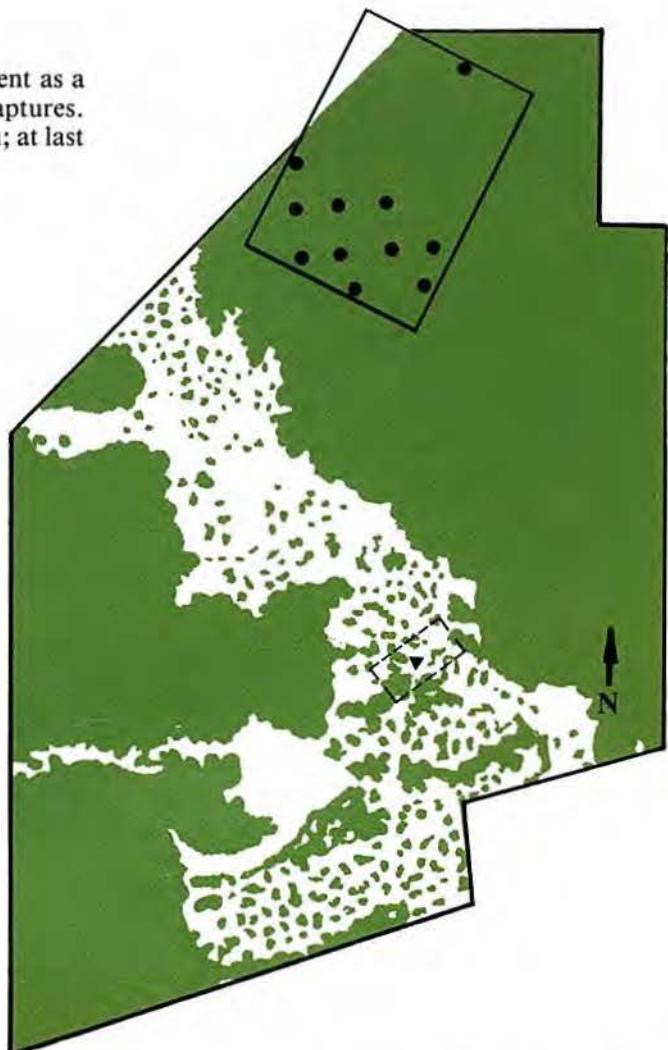
**Figure 5:** Home range of turtle No. 6015, male, showing movement as a juvenile before establishing permanent home range, 12 captures. Age and total length: at first capture, Age Class 1, 62mm; at last capture, Age Class 2, 122mm



Turtle No. 6015, 1974



Turtle No. 6015, 1982



- home range before movement, 1973, 0.4 acre (0.1 ha)
- home range after movement, 1974-1982, 5 acres (2 ha)
- ▲ capture site before movement
- capture site after movement
- woods
- open herbaceous field
- scale: 200 feet (61 m)

## **Relation of Population Density and Home-range Size to Vegetation and Major Vegetative Changes**

Figures 6 and 7 are aerial photographs of our study area at the beginning (1965) and near the end of our study (1981). Figure 8 shows density areas based on total turtle captures per acre for 1965 through 1970 (from Schwartz and Schwartz, 1974); Figure 9 shows this information for 1965 through 1980. Density areas in the latter figure were determined as in the earlier one, except that the values of the respective density areas are different because of the greater number of captures over the longer period of time.

The areas of highest turtle density (A and B) are similar in Figures 8 and 9, indicating that these areas continued to be used by the greatest number of turtles. Density Area A is still slightly larger than Area B and still has slightly higher numbers of turtles, but together they represent the core of turtle habitat on the study area. These lie in two woodlots of mixed deciduous hardwoods. Surrounding these areas of highest densities, and generally comprising woodland borders, are areas of somewhat lower densities, designated as Density Area C.

We did not appreciably alter these woodlots and their immediate borders during the 19-year study period, but there have been some ecological changes here. The undergrowth which came in as a result of practices prior to our ownership (grazing and logging for stave bolts) has in most places reached its maximum density and height and is beginning to regress, creating a slightly more open understory.

Density Area D, where it represents a ridge between the two main areas of turtle density, shows an increase in turtle utilization. In the early part of this study, this region was primarily open land which was utilized by turtles traveling between the two high-density areas. Over the years, this generally open land has become more heavily vegetated, primarily with numerous juniper trees (*Juniperus virginiana*). These trees create a pattern of interspersion, and turtles are often found resting under the junipers where they are shaded from the sun and protected by the spreading, ground-level branches. Some additional sprout growth of oak (*Quercus* sp.), hickory (*Carya* sp.) and persimmon (*Diospyros virginiana*) is common. Bushes of wild rose (*Rosa* sp.) and multiflora rose (*Rosa multiflora*) have also increased, adding to the interspersion of woody plants, but blackberry (*Rubus* sp.) has nearly disappeared. In addition to creating interspersion in the open areas, the encroaching woody plants have extended the borders of the wooded section into the open areas.

There have been changes, likewise, in the herbaceous cover of this open area. Much of the former predominant cover—ragweed (*Ambrosia* sp.) and goldenrod (*Solidago* sp.)—has been replaced by grass, mainly fescue (*Festuca* sp.), but also by small stands of Indian grass (*Sorghastrum nutans*) and bluestem (*Andropogon* sp.). In the denser herbaceous cover and grass, travel for turtles must be more

difficult, and turtles are seldom found where these stands are rank. Along with the vegetative changes, there are probably accompanying changes in food sources—fruits, insects and other invertebrates—that influence turtle use.

Turtles have not increased their use of Density Area D where it lies next to the southern border of our study area, although vegetative changes similar to those discussed above also have occurred there. We believe this is largely due to the automobile traffic on the road which borders this section of the study area. With the spread of housing around our study area, traffic has increased considerably on this narrow road with a resultant increase in turtle mortality. Turtles trying to live in this section are quickly eliminated if they wander onto the road, and turtles that might enter our study area from this direction are prevented from doing so.

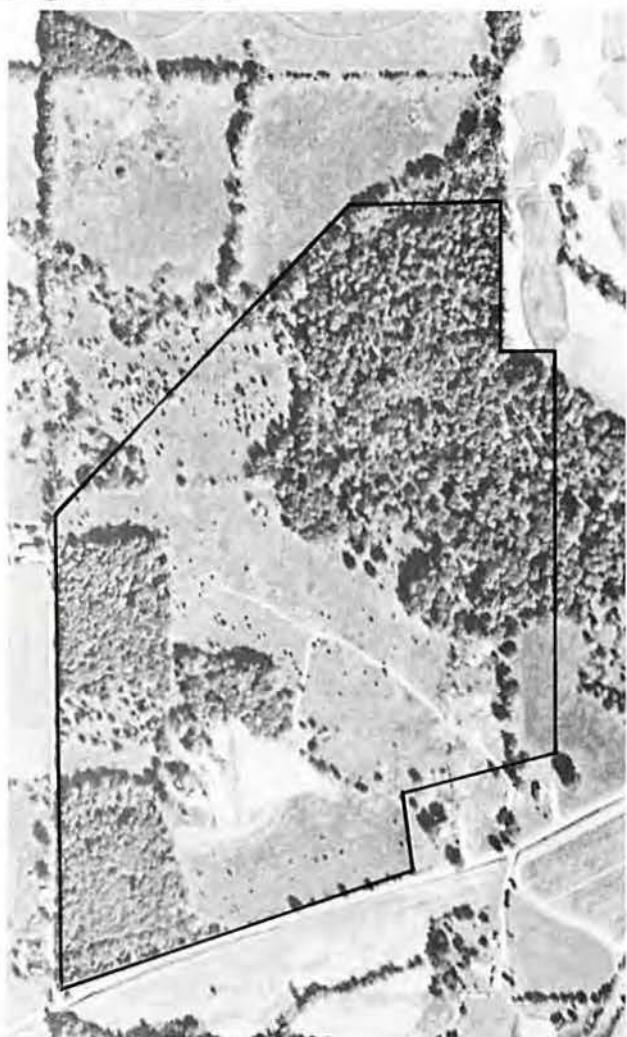
Density Area D, in the northern part of the study area and in adjacent areas outside the study area, shows an increase in turtle utilization owing to two factors. For one, we traversed this area more during the last three years of our study than in previous years and collected turtles living in the remaining portion of the woods and along the wooded stream. (This, however, did not affect our population estimates below, because these were computed only through 1980). But also, the larger open section, which we formerly eliminated from our study area because it yielded fewer than ten turtle captures per acre, has shown a decided change in vegetation with an accompanying increase in turtle utilization. Turtles collected in this area come from two sources—new individuals that have not been taken on the study area (probably entering from the west), and marked individuals that have extended their home ranges. Vegetative changes here are comparable to those discussed for the ridge between the two high-density areas.

We believe that once a turtle establishes a home range, it becomes so well acquainted with the features of it that gradual, successional changes in the vegetation are tolerated and have little influence on the home-range size. This is evidenced by the continuity of home-range occupancy by our 37 long-term, permanent residents. However, continued changes in plant succession in open fields, particularly an increase in aboreal species, may favorably affect the turtles' utilization of such areas and ultimately influence the size and location of the home ranges of turtles living in adjacent areas.

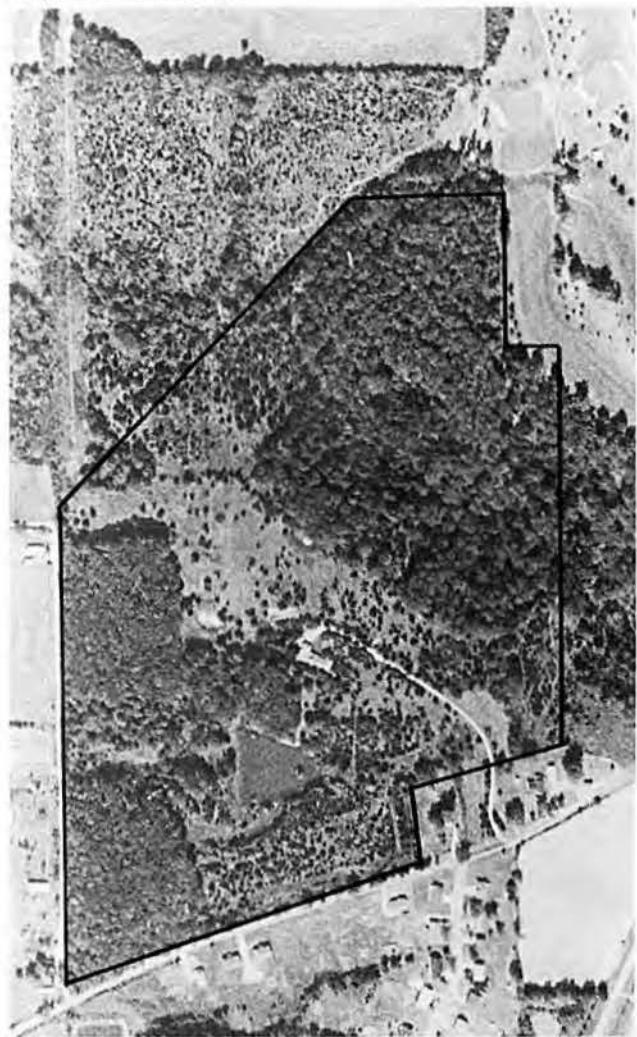
Stickel (1978) reports that no obvious changes occurred over 30 years in her study area, although the area might have become somewhat drier. Brush, logs and fallen tree branches still provided ample cover, and the canopy did not appear to have closed in appreciably.

**Figures 6 and 7:** Aerial photographs of study area

**Figure 6: 1965**



**Figure 7: 1981**



Changes in the vegetative cover over the 16 years are most conspicuous in the open fields.



Study area fields



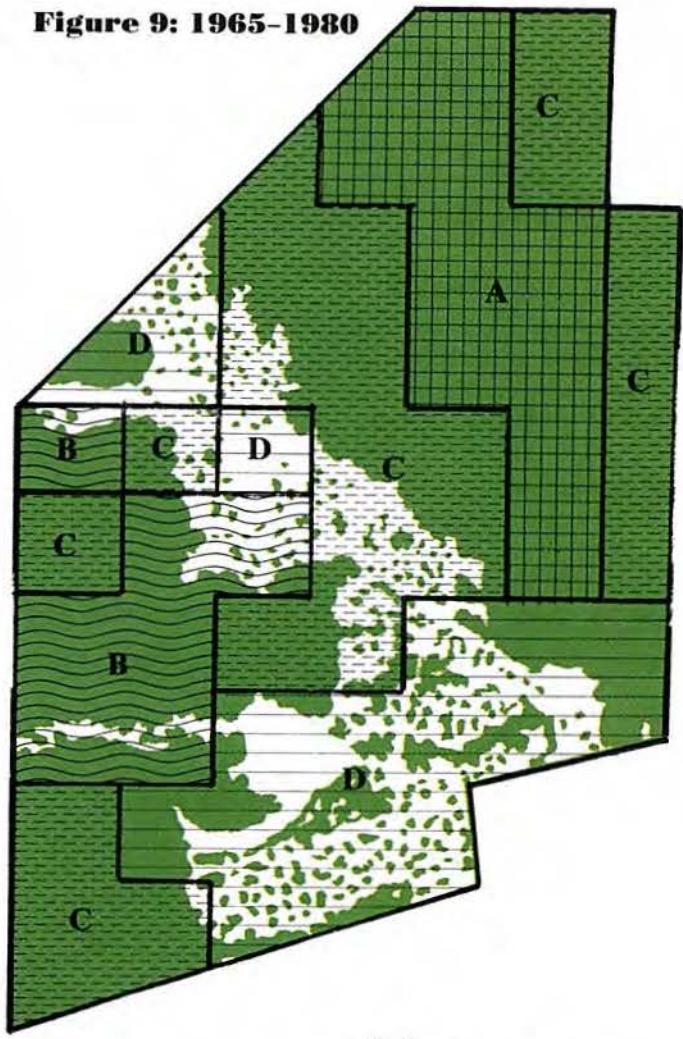
Study area woods

**Figures 8 and 9:** Density of turtle captures per acre superimposed on vegetative cover map of study area

**Figure 8: 1965-1970**



**Figure 9: 1965-1980**



	A = 60 or more
	B
	C = 20-59
	D = 11-19

	A = 120 or more
	B
	C = 40-119
	D = 21-39

woods  
 open herbaceous field  
 scale: 200 feet (61 m)

## MOVEMENTS

In our home-range and population studies, it is obvious that certain turtles are permanent residents and confine their activities to a particular area for at least 19 years and, we believe, probably a great deal longer. But not all turtles stay in our population. We find the marked shells of some turtles that have died. We know that some young turtles shift their residency before establishing a permanent home range, and this may explain why some young turtles come into and leave our area. But there are others we can-

not account for. We believe that some members of this group may live along the periphery of our area and come into it at infrequent intervals, while others are transients.

We consider a turtle to be a transient if it moves through the environment without returning to areas it previously used. To learn more about this segment of the population, we chose to study where and how far a transient moves, and to examine the age and sex of transients.

### Where and How Far a Transient Moves

Seven adult turtles, captured for the first time on our study area and considered to be likely transients, were equipped with radio transmitters (Kiester, Schwartz and Schwartz, 1982). Because of the intensity of our mark-recapture program, it is unlikely they had escaped detection earlier. We also selected and radio-tagged five adult turtles that had home ranges in the same part of our study area where these possible transients were collected. This latter group was considered a control; they continued to occupy their home ranges as they had done since they were first marked in 1965.

The seven that were taken for the first time proved to be of two types. Four had home ranges along the periphery of our area and only came onto our area infrequently. They were boundary residents. The remaining three, all males, subsequently proved to be true transients.

We followed No. 8071 (140mm in total length, and estimated to be a minimum of ten years old) from 1 May 1976 to 4 July 1977. This turtle stayed on our study area for a week after receiving his transmitter, then suddenly started to travel southeast (Figure 10). As he did so, he crossed the road that bounds our land, crossed a cut and wind-rowed alfalfa field, and passed through a pasture to a rugged intermittent drainage. During the hot weather of July, he used a fescue hayfield; in August, he traveled on to a small oak-hickory woods surrounded by a hog-proof fence. Although he tried to penetrate the fence at many places, it took him nearly a month of intermittent activity, frequently backtracking for a hundred feet (30.5 m) or so, to find a loose point in the wire and dig under. He crossed another road, traveled through the backyards of a subdivision and on 31 October went into hibernation in a patch of oak-hickory woods four miles (6.4 km) from his first capture point. On 12 April 1977, he resumed his travels, still moving southeast. He moved up and down a stream bank for about five weeks before finally slipping into the water and swimming 25 feet (7.6 m) to the opposite bank. As his travels continued to take him farther from our study area, we decided to remove the radio and let him continue on his way undetected. During this 15-month period, he traveled



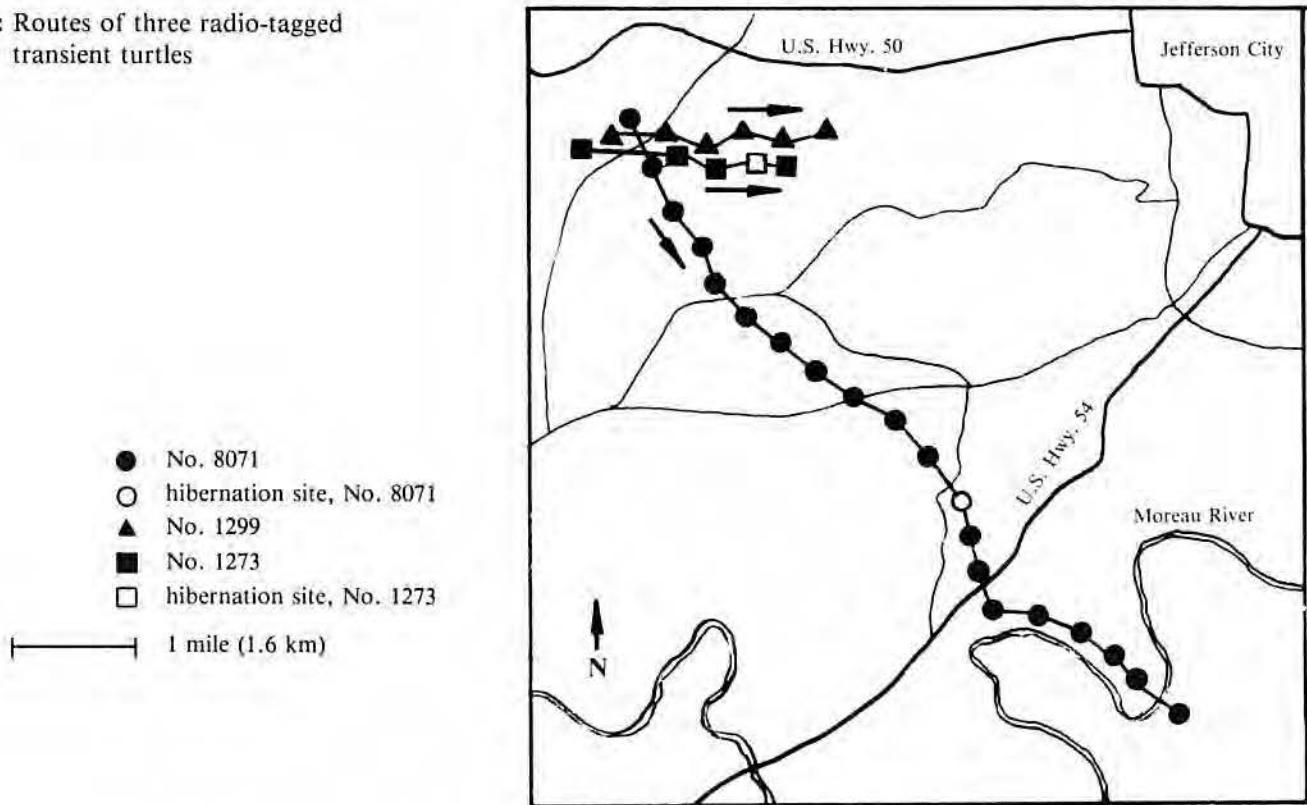
Turtle No. 8071 crosses Mo. Hwy. C, Cole County

a straight-line distance of 6.2 miles (10.0 km) in the same southeasterly direction. We observed him mating with two different females he encountered en route and saw him in the company of four other females.

We followed another transient, No. 1273 (131mm in total length; minimum estimated age, 25 years), from 24 May 1977 to 8 May 1978 (Figure 10). For the first three months, this turtle remained in a small area (4.9 acres, 1.9 ha) in the vicinity of his capture. Then he moved east in a straight line for 1.1 miles (1.7 km). He crossed our boundary road, passed through some second-growth timber and finally reached a patch of open oak-hickory woods. Here he hibernated from early November until the following spring. After emergence, he stayed in the same vicinity for a few weeks, then was lost due to transmitter failure. During his travel, he was observed to mate with three different females.

The third transient, No. 1299 (130mm in total length; minimum estimated age, 12 years) traveled east for 1.7 miles (2.7 km) from 26 July 1977 to 14 September 1977 (Figure 10). He also crossed our boundary road and entered some second-growth timber. Here he apparently was captured by someone who removed the transmitter and hung it on a fence.

**Figure 10:** Routes of three radio-tagged transient turtles



### Age and Sex of Transients

In the spring, following emergence from hibernation—and particularly during a warm, rainy spell—turtles frequently travel across highways. They also cross highways during summer and fall but not as often as during spring. Many are killed by traffic, and their remains are common on roads and roadsides. We believe that areas along highways do not have a large permanent population of turtles, since individuals living there would soon be eliminated by traffic. Thus, turtles crossing highways are likely to be transients, and a highway is just another obstacle in their path.

We wanted to determine the age and sex of turtles crossing highways. During the last two weeks of April 1981 and the first two weeks of May 1982, we collected 74 dead

turtles on or along highways in Cole County, where our study area is located. In Class 1 there were 17 males, 15 females and one unsexed; in Class 2 there were 22 males and five females; in Class 3 there were six males, no females and one unsexed; an additional seven males were not aged. From this small sample we concluded that half the turtles crossing highways are young and are divided almost equally between the sexes. About half are adults, and among these are many more young adult males (Class 2) than older adult males (Class 3) or females. Some females may take trips outside their home range, presumably for egg-laying (Stickel, 1950), but the highway-killed females we collected did not contain mature eggs.

### Importance of Transients

Although transients have been suspected to occur in other animal species, their presence has not been demonstrated because of methodological limitations. We feel that our study, which combines radio-tracking and mark-recapture, has permitted us to identify with certainty the occurrence of transients in our population.

What physiologically motivates a turtle to become a transient is unknown. We believe that turtles are transients at certain times in their lives. Some young turtles—the juvenile transients—apparently move about for a period of time before establishing a home range, but this is not true for all young turtles. Then there appears to be a time in the

lives of males, particularly when they are young adults and presumably in the early years of sexual activity, when some individuals undertake extensive movements. But again, this is not true for all young males, as evidenced by our home-range study of long-term, permanent residents.

Adult male transients probably comprise only a small segment of a population, but they are highly important, as evidenced by their mating. They are the mechanism by which genes are transferred from one sedentary population to another separate population and are thus influential in the evolution of the species.

## POPULATION

In our 1974 paper, we estimated that our study area had a high population of 600 to 700 turtles and a low of 400. We believe we have a good sample of the population because of the efficient collecting by our keen-nosed dogs. We also consider our study-area population to be representative of similar turtle habitats in central Missouri as determined by sample counts made with our dogs.

By applying the Jolly-Seber stochastic mark-recapture model (Seber, 1973) to the first 16 years of our study, we estimated the population to fluctuate between approximately 400 and 600 turtles (Table 2). The fluctuations generally are small, and we believe that the population has remained fairly stable. During this period, new turtles entered the population (the estimated number varied from 27 to 134 annually), and obviously a nearly comparable number left the population.

The estimated number of the sexes by year is approximately equal.

The estimated percentage of the three age classes by year is as follows: Class 1 comprises approximately 46 percent; Class 2, 37 percent; and Class 3, 17 percent.

Figure 11 shows the percentage of different individuals in the population by year. After the first two years required to mark our population, the percentage of new turtles entering the population varied from six to thirty-seven. The greatest loss of any segment occurred in the year following the initial capture. This indicates that many of these turtles may have moved on (see Transients). Loss of any segment was not great thereafter, and death

probably became the primary cause of population decline in later years. It is interesting that each year's population contains some turtles marked in all of the preceding years, showing that some of the turtles entering a population stay and become permanent residents. (In a few years' collections, representatives of certain previous years were not captured. This probably is due to the size of our sample, because some of these individuals were recovered in subsequent years.)

Once a turtle is present in the population, its average probability of survival to the next year (and therefore of remaining in the population) is 81.9 percent, varying from 74 to 92 percent by year. When this is examined by age class, the percentages are as follows: Class 1, 66.3 percent (from 43 to 91 percent); Class 2, 83.4 percent (from 68 to 96 percent); and Class 3, 85.6 percent (from 61 to 105 percent).

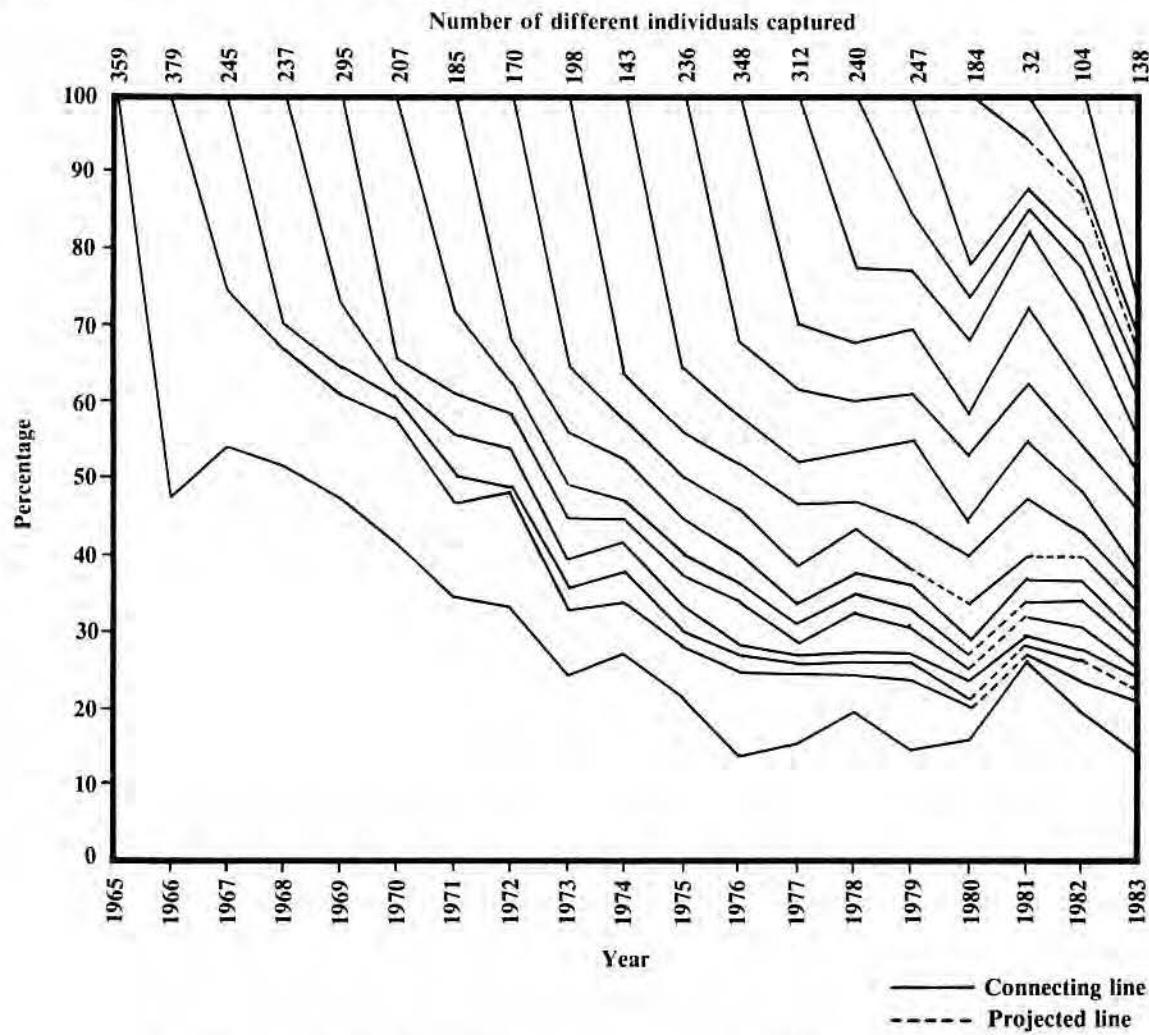
We also reported (Schwartz and Schwartz, 1974) that "it will take approximately 14 years for the turtles marked in 1965 and 1966 to become an insignificant part of the population." Now, after 19 years, this segment of the population comprises about 25 percent of the total. Obviously, it will take considerably longer for all of the turtles marked in any one year to disappear from the population.

Survival in our population appears to be lower than that reported by Stickel (1978). Of her turtles that were 20 or more years old at the time of marking, she showed a survival of 40 percent 20 years after marking and 13 percent 30 years after marking.

**Table 2:** Estimated number of turtles in the population and estimated number of new turtles entering the population (Jolly-Seber stochastic mark-recapture model)

Year	Estimated number of turtles in population	Standard error of estimated number of turtles in population	Estimated number of new turtles entering population	Standard error of estimated number of new turtles entering population
1965	—	—	—	—
1966	597	26	45	20
1967	492	21	93	18
1968	484	21	78	16
1969	477	18	134	23
1970	527	32	48	22
1971	444	25	72	21
1972	409	22	97	24
1973	460	25	89	29
1974	469	30	76	28
1975	492	21	82	20
1976	539	17	118	17
1977	553	22	56	17
1978	497	23	27	15
1979	475	33	—	—
1980	—	—	—	—

**Figure 11:** Percentage of turtles in the population by the year marked, 1965–1983.<sup>4</sup>



**Note:** The small sample in 1981 is probably responsible for the larger increases shown in this year.

<sup>4</sup>The total numbers here are somewhat smaller than those for a similar chart in our 1974 paper because we do not include those turtles for which we have incomplete data on age and sex.

Survival takes on many aspects. Turtles have always faced certain natural problems. We find some blind, with ear infections, covered with mites, with their shells chewed or otherwise damaged and limbs amputated. Eggs, hatchlings and very young turtles are easy fare for all sorts of predators. Hibernation is a critical time; conditions vary from year to year, and a lack of rain in the fall may prevent turtles from digging deep enough to survive a sudden cold spell; too early a spring may arouse them before the last freeze has passed. Heat and drouth may affect their food supply and their well-being, especially since many have home ranges where there is no permanent source of water. Forest and brush fires destroy their habitat and kill and maim these animals.

Once turtles become permanent residents and the environment remains fairly undisturbed, they simply con-

tinue to live out their lives. And because three-toed box turtles are long-lived, this residency may extend for several decades and even to a half-century or more.

But what if the environment is disturbed? These natural problems pale in the face of human needs in our modern world. Turtle habitat, similar to that of our study area, is rapidly being torn up and destroyed. There are about 44 houses across our boundary road to the south, while just beyond our boundary to the west there now are 300 houses. The traffic on our road has increased about one thousand percent. Multiply these effects of increased urbanization on a greater scale across turtle habitat generally and across the expanding network of highways in our state and they impose a genuine burden on this species, which has a low rate of reproduction and population renewal.



Covered with mud, a turtle emerges from hibernation to begin yet another year of life. With habitat rapidly disappearing, what may the future hold for its kind?

---

## LITERATURE CITED

- Burghardt, Gordon M. 1977. Learning processes in reptiles. Pages 555-681 in C. Gans and D. W. Tinkle, eds. *Biology of the Reptilia*. Vol. 7. Academic Press, New York.
- Carr, A. 1952. *Handbook of Turtles: The Turtles of the United States, Canada, and Baja California*. Cornell Univ. Press, Ithaca. 542 pp.
- Castell, D. B. 1911. The discriminative ability of the painted turtle. *Journ. Animal Behavior* 1:1-28.
- Conant, R. 1975. *A Field Guide to Reptiles and Amphibians of Eastern and Central North America*. Houghton Mifflin Co., Boston. 429 pp.
- Dolbeer, R. A. 1969. A study of population density, seasonal movements and weight changes, and winter behavior of the eastern box turtle, *Terrapene c. carolina* L., in eastern Tennessee. M.Sc. thesis, Univ. Tenn. 53 pp.
- Ernest, C. H., and R. W. Barbour. 1972. *Turtles of the United States*. Univ. Press of Kentucky, Lexington. 347 pp.
- Evans, L. T. 1952. Endocrine relationships in turtles III. Some effects of male hormones in turtles. *Herpetologica* 8 (2):11-15.
- Ewing, H. E. 1939. Growth in the eastern box turtle, with special reference to the dermal shields of the carapace. *Copeia* 1939 (2): 87-92.
- Kiester, A. R. 1977. Communication in amphibians and reptiles. Pages 519-544 in T. A. Sebeok, ed. *How Animals Communicate*. Indiana University Press, Bloomington.
- Kiester, A. R., C. W. Schwartz and E. R. Schwartz. 1982. Promotion of gene flow by transient individuals in an otherwise sedentary population of box turtles (*Terrapene carolina triunguis*). *Evolution* 36:617-619.
- Legler, J. M. 1960. Natural history of the ornate box turtle, *Terrapene ornata ornata* Agassiz. Univ. of Kansas Publ. Mus. Nat. Hist. 11 (10):527-669.
- Leuck, B. E., and C. C. Carpenter. 1981. Shell variation in a population of three-toed box turtles (*Terrapene carolina triunguis*). *J. Herpetology* 15:53-58.
- Madden, R. 1975. Home range, movements, and orientation in the eastern box turtle, *Terrapene carolina carolina*. Ph.D. thesis, City University of New York. 217 pp.
- Milstead, W. W. 1969. Studies on the evolution of box turtles (Genus *Terrapene*). *Bull. Florida State Museum Biol. Series* 14 (1):1-113.
- Nichols, J. T. 1939. Data on size, growth, and age in the box turtle, *Terrapene carolina*. *Copeia* 1939 (1):14-20.
- . 1940. Eye color in the box turtle (*Terrapene carolina*). *Copeia* 1949 (2):130.
- Pope, C. H. 1939. *Turtles of the United States and Canada*. Knopf, New York. 343 pp.
- Reagan, D. P. 1974. Habitat selection in the three-toed box turtle, *Terrapene carolina triunguis*. *Copeia* 1974 (2):512-527.
- Schwartz, C. W., and E. R. Schwartz. 1974. The three-toed box turtle in central Missouri: its population, home range, and movements. Mo. Dept. Cons., Terr. Ser. No. 5:28 pp.
- Seber, G. A. F. 1973. *The Estimation of Animal Abundance*. Griffin, London. 506 pp.
- Stickel, L. F. 1950. Populations and home range relationships of the box turtle, *Terrapene c. carolina* (Linnaeus). *Ecol. Monogr.* 20:351-378.
- . 1978. Changes in a box turtle population during three decades. *Copeia* 1978 (2):221-225.

---

## ACKNOWLEDGEMENTS

We wish to acknowledge, again, the initial contribution of our American water spaniel, Drake I, and the efforts of our willing Labrador retrievers—Andy, Brant, Jet, Tara, Drake II, Otter, Smudge, Raven and Buck—who were responsible for approximately 6,000 of the 6,789 turtle captures. Also, we thank the Missouri Department of Conservation for publishing this paper—and especially Michael McIntosh for his genuine interest and his invaluable assistance in editing. Mr. and Mrs. Henry Andrae, Mr. and Mrs. Ed Loeffler, and Mr. and Mrs. Tom Vetter generously allowed us to extend our study area onto their property.

ERS and CWS were biologists with the Missouri Department of Conservation for 31 and 41 years, respectively; they are now retired. ARK currently is Assistant Professor of Biology at Tulane University, New Orleans, Louisiana.



## THE MISSOURI DEPARTMENT OF CONSERVATION TERRESTRIAL SERIES

The Terrestrial Series is published by the Missouri Department of Conservation to make available the results of original investigations of the terrestrial environment of Missouri. It originally was designated the Technical Bulletin Series. Numbers published to date include:

1. The Ecology and Management of the Wild Turkey in Missouri. Paul Dalke, A. Starker Leopold and David L. Spencer. 1946. 86 pp. (Out of print)
2. Some Aspects of Missouri Quail and Quail Hunting, 1938-1948. Rudolf Bennett. 1951. 51 pp. (Out of print)
3. Canada Geese of the Eastern Prairie Population, With Special Reference to the Swan Lake Flock. Richard W. Vaught and Leo M. Kirsch. 1966. 91 pp.
4. Wildlife Foods and Understory Vegetation in Missouri's Natural Forests. Dean A. Murphy and Hewlette S. Crawford. 1970. 47 pp.
5. The Three-Toed Box Turtle in Central Missouri. Charles W. Schwartz and Elizabeth R. Schwartz. 1974. 28 pp.
6. Food and Nutrition of Cottontail Rabbits in Missouri. Leroy J. Korschgen. 1980. 16 pp.
7. Missouri Fur Harvests. Frank W. Sampson. 1980. 59 pp.
8. Ecological Studies and Management of Missouri Bats, with Emphasis on Cave-dwelling Species. Richard K. LaVal and Margaret L. LaVal. 1980. 56 pp.
9. Radiotelemetry Studies of the Mourning Dove in Missouri. Mark W. Sayre, Thomas S. Baskett and Kenneth C. Sadler. 1980. 20 pp.
10. Lead Poisoning and Lead/Steel Shot: Missouri Studies and Historical Perspective. Dale D. Humburg and Kenneth M. Babcock. 1982. 24 pp.
11. The Status, Distribution, and Habitat Preferences of the Birds of Missouri. Richard L. Clawson. 1982. 80 pp.
12. The Three-Toed Box Turtle in Central Missouri, Part II: a nineteen-year study of home range, movements and population. Elizabeth R. Schwartz, Charles W. Schwartz and A. Ross Kiester. 1984. 28 pp.

